

but the resemblance goes no further, and *C. hintonii* probably does not have a particularly close relationship to *Alophia* or *Ainea*.

Little attention has been paid to the broad connective condition in Iridaceae, and although it seems intuitively to be apomorphic, the character is distributed in two of three genera of Maricaceae and several species of *Cypella*, possibly the basal genus of Tigridiaceae. Thus, a broad connective is probably synapomorphic for the clade that includes Maricaceae and Tigridiaceae (see Goldblatt, 1990) but plesiomorphic for *Ainea* and *Alophia*, although the pandurate shape in *Alophia* seems unique. There no longer seems any reason to place *Alophia* in Tigridiaceae. The shared polyploid base number is almost certainly convergent, and *Alophia* does not have either the united filaments or bisulcate pollen grains that are apomorphic for Tigridiaceae. Beyond a possible close relationship with *Ainea*, the affinities of *Alophia* seem more uncertain than ever.

DISTRIBUTION AND SPECIES REVIEW

Alophia occurs across a wide portion of temperate and tropical America. The most well known and widespread species, *A. drummondii* (Graham) R. Foster (synonyms *Eustylis purpurea* (Herbert) Engelm. & Gray, *E. punctata* (Herbert) Ravenna), extends from the southern United States (Arkansas, Louisiana, Oklahoma, and Texas) to southern Mexico (including Vera Cruz, Chiapas, and Tabasco) (Goldblatt, 1974; Henrich & Goldblatt, 1992). The species, or one closely related to it, also occurs in Guyana (cf. Maas et al. 1774, U). This seems to have slightly smaller flowers, filaments united in the lower half, and style branches that are shorter and do not arch over the stamens. A second species, the smaller-flowered *A. silvestris* (Loesener) Goldblatt (synonyms *Nemastylis bequaertii* Standley, *A. rotacea* Ravenna), is restricted to Central America, where it extends from southern Mexico to Costa Rica. A third species, *A. medusa* (Baker) Goldblatt (basionym *Chlamydstylis medusa* Baker), apparently poorly known, occurs in Goiás, central Brazil. It is particularly distinctive in its large flowers and spathes (tepals 2.5–3 cm long, inner spathes 6 cm), a conspicuous band of glandular tissue in the median of the inner tepal limbs, and terete leaves. To these the new *A. veracruzana* can now be added. This has a restricted distribution in northeastern Mexico, currently known only from Vera Cruz.

One species, *Alophia intermedia* Ravenna (1964) (known to us only from the description) from Sinaloa in western Mexico, may be misplaced

in the genus. It reportedly has pendent lilac-violet flowers with a yellow center, connate filaments, pandurate anthers, and deeply forked style branches, the arms of which are 14–15 mm long. In the article in which he described *A. intermedia*, Ravenna (1964) included *A. triflora* in *Alophia*, a species now regarded as conspecific with *Tigridia meleagris* (Molseed, 1970). Examination of the type of *A. intermedia*, not available to us, is necessary before its status and generic position can be assessed.

Alophia veracruzana seems most closely related to *A. drummondii*, which it resembles in the size and general form of the flower (Figs. 1A, 2A). *Alophia drummondii* is normally a taller plant, and the flowers are violet to red-purple with the well-differentiated tepal claws marked cream to yellow and densely speckled throughout with dark red-purple. The major difference between the two species lies in the shape of the inner tepals. In *A. drummondii*, the inner tepals are narrower than the outer tepals, and the limbs are sharply bent at the base (Fig. 2A). The edges of the lower part of the inner tepal limbs are closely pinched together below where they are whitish to yellow and arched over the median lower part of the limb. This fold covers a narrow median zone of stalked glandular, presumably nectariferous tissue. The distal part of the outer tepal limb is dark red-purple and ascending. *Alophia veracruzana* (Fig. 1A) lacks a clear distinction of tepal claw and limb, and the inner tepals, as wide as the outer and with lightly undulate margins, have no nectariferous band.

SYSTEMATICS

***Alophia veracruzana* Goldblatt & Howard, sp. nov.** TYPE: Mexico. Vera Cruz: sandy roadside south of Alvarado, cultivated Missouri Botanical Garden, June 1990, Goldblatt & Howard 9070 (holotype, MEXU; isotypes, K, MO). Figure 1.

Plantae 25–30 cm altae, bulbis anguste ovoideis, tunicis atrobrunneis, foliis 4–5, laminis plicatis, 5–8 mm latis, rhipidiis 4–5 florum, spatha interiore 32–38 mm longa, floribus lilacinis tepalis interioribus maculis albis vel luteis notatis, tepalis obovatis obscure unguiculatis, exterioribus 17–20 mm longis, ca. 10 mm latis, interioribus 16–19 mm longis, ca. 10 mm latis, staminibus atropurpureis, filamentis ca. 2 mm longis infra contiguis, antheris anguste panduratis, latrorsis, ca. 4 mm longis, 1.1 mm latis infra, ca. 2 mm supra.

Perennial geophyte 25–30 cm high. *Bulbs* narrowly ovoid, the scales dark brown. *Leaves* 4–5, laminate except the uppermost ± entirely sheathing and elaminate, blades plicate, mostly about as

long to slightly longer than the stems, the lower 2–3 inserted below the ground, the upper two inserted well above ground, the lower of these near the base and the upper near the midline and shortest, narrowly lanceolate (to almost linear), 5–8 mm at the widest, apices attenuate. *Stem* terete, generally with one branch produced in the upper third, subtended by the sheathing leaf. *Inflorescences* rhipidia, single and terminal, usually 4–5-flowered; *spathes* green, attenuate, the apices generally dry and light brown, unequal, the inner 32–38 mm long, the outer about $\frac{2}{3}$ as long. *Flowers* secund, the pedicels about $\frac{2}{3}$ as long as the inner spathe, curved outward at the apex; *perianth* actinomorphic, pale to dark lilac-purple (rarely whitish), paler toward the center and lightly flecked toward the margins with darker purple, the inner tepals with undulate margins and each with a pair of large white to yellow marks near the base of the limbs, with a weak spicy-sweet scent; *tepals* free, \pm obovate, claws weakly differentiated and spreading outward, outer tepals 17–20 mm long, the limbs spreading, ca. 10 mm wide, inner tepals 16–19 mm long, ca. 10 mm wide, the limbs held at \pm right angles to the claws and with the lower lateral areas raised and the median portion recessed. *Stamens* dark purple, filaments ca. 2 mm long, broader and contiguous below, narrow in the upper half; *anthers* coherent at their bases, with a broad narrowly pandurate connective narrowest in the middle $\frac{2}{3}$, weakly ascending, ca. 4 mm long, 1.1 mm wide at the base, nearly 2 mm at the apex, sporangia marginal and nearly latrorse; pollen yellow, broadly sulcate. *Ovary* narrowly obovoid, ca. 4 mm long, exerted from the spathes; *style* ca. 5.5 mm long, dividing opposite the middle of the anthers into three thickened branches, the branches erect, ca. 1.5 mm long, each dividing into two long ascending-recurved arms, these ca. 3 mm long, tubular, stigmatic apically, arching over the anthers. *Capsules* obovoid-oblong, trigonous and truncate, 14–24 mm long; *seeds* 1.8–2.0 \times 1.3–1.5 mm, obovoid-pyriform, narrowest at the micropylar end, the chalazal end concave, lightly rugose, yellow-brown. *Chromosome number* $2n = 28$ (Goldblatt & Howard 9070).

FLOWER PHENOLOGY AND COMPATIBILITY

As in all Tigridiaceae, the fugacious flowers last only one day. Flower buds appear the day before flowering, and the tepals enlarge to their full size during the night. Early in the day the outer tepals unfold, but until 7 A.M. the inner tepals remain closed over the style and stamens. The inner tepals

begin to separate at about 8 A.M., and by 9 A.M. they have spread sufficiently to allow access to the style and stamens; by this time the anthers have dehisced, revealing the bright yellow pollen. At about 10 A.M. the inner tepals reach their full open position. The tepals begin to collapse at about 2:30 P.M., and by 3:30 P.M. are closed together. Like its relative *A. drummondii*, *A. veracruzana* is self-compatible. Self-fertilization often occurs in one or two flowers of a rhipidium with resultant capsule and seed production. As the stigmas are not in contact with the anthers while the flowers are open, pollination presumably occurs after the flowers collapse, when the parts of the flowers are pushed together by the inward-falling tepals. Outcrossing is presumably the normal mode of reproduction for the species in view of the colorful and fragrant perianth. The occasional selfing presumably serves to ensure seed production in the absence of insect-mediated pollination. Plants of *A. veracruzana* can be raised from seed to flowering in a single growing season. Seeds sown in late fall in the greenhouse in St. Louis grew to flowering size in about six months.

KARYOLOGY AND POLLEN MORPHOLOGY

Chromosome number in *Alophia veracruzana* is $2n = 28$. Four long chromosomes, one pair submetacentric and the other acrocentric, contrast markedly from the 12 remaining much smaller pairs. The karyotype accords with that of the tetraploid members of Tigridiaceae (Goldblatt, 1982; Kenton & Heywood, 1984).

The pollen grains have a single broad sulcus as long as the grains when fully expanded (Goldblatt & Le Thomas, in prep.) and resemble those of *A. drummondii* (Goldblatt, 1974). The grains of *Alophia* thus correspond with those of the majority of Tigridiaceae excluding Tigridiaceae (*Tigridia*, *Fosteria*, *Sessilanthera*, and *Cobana*—Molseed, 1970; Ravenna, 1974), which have bisulcate grains.

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CHROMOSOME NUMBER IN *TICODENDRON* (FAGALES, TICODENDRACEAE)

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ABSTRACT

The chromosome number of *Ticodendron incognitum* is reported for the first time as $2n = 26$, and the phylogenetic significance of this number within Fagales is discussed.

After exhaustive collaboration among several authors (Hammel & Burger, 1991) the monotypic family Ticodendraceae was described (Gomez-Laurito & Gomez P., 1991) to accommodate the Mesoamerican tree *Ticodendron incognitum* Gomez-Laurito & Gomez P. (1989). Evidence from wood anatomy (Carlquist, 1991), leaf anatomy (Hickey & Taylor, 1991), floral anatomy and morphology (Tobe, 1991), pollen (Feuer, 1991), and sieve element characters (Behnke, 1991) strongly suggests its inclusion in Fagales. We report for the first time the chromosome number of *Ticodendron incognitum* as $2n = 26$ and discuss the possible phylogenetic significance of this number within Fagales.

MATERIALS AND METHODS

Root tips were collected at approximately 9:30 A.M. from a single specimen growing in the greenhouses at the Missouri Botanical Garden (Voucher: Hammel & Rivera 17834, MO). After pretreatment with aqueous 1-bromonaphthalene for 4 hours, the tips were fixed in 3:1 ethanol (95%)–glacial acetic acid. After hydrolysis in 10% HCl for 7 minutes at 70°C, root tips were squashed in FLP orcein (Jackson, 1973).

DISCUSSION

The diploid number of $2n = 26$ and small, relatively uniform chromosomes of *Ticodendron incognitum* corroborate the results cited above that indicate the distinctness of this taxon from other families of Fagaceae.

The Fagales (sensu Cronquist, 1981) have base numbers $x = 8, 11, 12, 13,$ and 14 (Raven, 1975). In Fagaceae $x = 12$ predominates, occurring in

Castanopsis, *Cyclobalanopsis*, *Fagus*, *Castanea*, *Lithocarpus*, *Pasania*, and *Quercus* (Mehra & Hans, 1969; Raven, 1975; Morawetz & Samuel, 1989), while *Trigonobalanus* has $x = 21$ or 22 (Hou, 1971; Soepadmo, 1972). *Colombobalanus* and *Formanodendron*, segregated from *Trigonobalanus* by Nixon & Crepet (1989), remain uncounted in the family. *Nothofagus*, which may merit its own family (Nixon, 1982), has $x = 13$ (Armstrong & Wylie, 1965; Ono, 1977). Within Betulaceae *Carpinus*, *Ostrya*, and *Ostryopsis* form a distinct, evidently paleodiploid group with $x = 8$ (Raven, 1975; Löve & Löve, 1982); *Betula*, *Alnus* (Raven, 1975), and *Duskechia* (Kovanda, 1984; Pashuk, 1987) have $x = 14$; *Corylus* may have $x = 14$ (records of $2n = 28$ require confirmation), but there are records of $n = 11$ in the genus as well (e.g., Löve & Löve, 1982). The monogeneric Balanopaceae appear to have $x = 20$ (Morawetz & Samuel, 1989) (the single count of $n = 21$ in *B. australina* (Goldblatt, 1979) may be erroneous).

Clearly, $x = 13$ is infrequent in Fagales. Our count of $2n = 26$ from a single plant suggests $x = 13$ for Ticodendraceae, so within the order Ticodendron shares this number only with *Nothofagus*, a genus from which it is distinct.

Although Raven (1975) proposed $x = 7$ as basic for Fagales, a plausible scenario for chromosomal evolution can be suggested based on $x = 8$. Assuming $x = 8$, presumed base number in the closely related Hamamelidales as well (Goldblatt & Endress, 1977; Morawetz & Samuel, 1989), for the early members of Fagales, dysploid reduction to $x = 7$, followed by a doubling to 14 and subsequent reduction to 13, 12, and 11 seems to us the most reasonable explanation for change within extant members of the order. The base number $x = 13$,

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common to *Ticodendron* and *Nothofagus*, was most likely achieved independently from $x = 14$, a hypothesis supported by significant differences in wood anatomy (Carlquist, 1991), reproductive morphology (Tobe, 1991), leaf architecture (Hickey & Taylor, 1991) and other features. We note, however, the comment by Tobe (1991: 141) that *Nothofagus* is the best candidate in comparing Fagaceae with *Ticodendron*, which is at least superficially similar in a number of important characters.

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